POLYCHROMATISM IN SNAKES

Wilfred T. Neill

The present paper explores the topic of polychromatism in snakes. It is convenient to begin the discussion with the California kingsnake, for this reptile affords virtually the only case of ophidian polychromatism to have been fairly well studied in the past.

Herpetologists once recognized two sympatric species of kingsnakes, belonging to the *Lampropeltis getulus* group, in southern California. One of these, with a ringed pattern, was known scientifically as *L. g. boylii* (Baird and Girard); the other, with a lineate pattern, generally stood as *L. californiae* (Blainville). The two did not differ other than in pattern, and apparent intermediates were known. Even before the 20th Century it was suspected that the two were but phases of a single form.

Klauber (1936, 1939) showed that a ringed, a striped, or an intermediate (partially striped) female could produce a brood that included both ringed and striped individuals. He classified three kinds of "aberrant" patterns, phenotypically intermediate between ringed and striped; and held that ringed and striped examples were but pattern phases of a single taxon, to be called *Lampropeltis getulus californiae.* He also pointed out other, possibly comparable, cases of dichromatism in snakes, i.e. *Masticophis flagellum frenatum* and *M. piceus, Phyllorhynchus d. decurtatus* and *P. browni, Sonora semiannulata* and *S. miniata.*

Smith (1943) advanced a view contrary to that of Klauber, holding the ringed and striped kingsnakes to be two distinct species, and the intermediates to be hybrids between them. Klauber (1944) offered a rebuttal. Klauber's interpretation was favored by Mayr (1944) from the standpoint of taxonomic theory, and by L. C. Dunn (1944) from that of genetic theory. Nevertheless, Smith and Taylor (1945) maintained *Lampropeltis californiae* as a species distinct from *L. getulus boylii.* Smith (1952b) later held that *L. californiae* and *L. g. boylii* "were clearly species formerly, but now have so coalesced that they cannot be separately recognized at the present time level." There has been no further contribution to the problem, although most herpetologists have accepted Klauber's taxonomic arrangement.

THE LINEATE PATTERN IN EASTERN KINGSNAKES

Some previous students have been unaware that the lineate, "*californiae*" pattern is often suggested, and sometimes duplicated, in subspecies of *Lampropeltis getulus* inhabiting the eastern United States. In the subsequent discussion, I have followed other authors in describing the usual kingsnake pattern as "ringed," although the term is a misnomer since the transverse light markings are not complete ventrally.

The most easterly subspecies of the kingsnake is *Lampropeltis getulus sticticeps* Barbour and Engels (1942) from Okracoke Island, North Carolina. For unstated reasons the subspecies was synonymized with *L. g. getulus* by Schmidt (1953). Whatever the taxonomic status of the form, the type specimen had a tendency toward a lineate pattern in that there was a series of elongate spots on the neck and also on the tail, although the midbody was ringed. This individual recalls the *californiae* intermediates, of which Klauber (1939) stated, "Usually the striped sections are present at the head and tail, while the mid-body is ringed."

Lampropeltis g. getulus (Linnaeus), as currently defined, ranges from southern New Jersey southward into northern Florida, and westward as far as the Appalachian Mountains and southern Alabama. Specimens from above the Fall Line exhibit a blackish ground color with narrow, whitish rings; rarely is there any pronounced tendency toward lineate markings. Individuals from below the Fall Line, in Georgia and northeastern Florida, usually display a brownish-black ground color with slightly wider, yellowish rings; but often there is a middorsal line on the neck, extending posteriorly for as much as a quarter of the reptile's total length. Blanchard (1921) examined a kingsnake from eastern Virginia in which the rings were replaced by elongate spots, suggesting a vertebral light stripe. Blanchard emphasized the similarity of this example to some lineate *L. g. californiae*, but his remarks seem to have been overlooked by later students.

At the base of the Florida panhandle occurs *Lampropeltis getulus goini* Neill and Allen, marked with broad, blotch-like rings (Fig. 1, A). Of the more easterly subspecies of the kingsnake, this one shows the most frequent and the best development of a lineate pattern. All but five or six specimens, of 70 seen (including intergrades with *L. g. getulus*), showed at least a slight tendency toward striping (Fig. 1, B), and about 20 were as well striped as *californiae* intermediates described and figured by Klauber (Fig. 1, C).

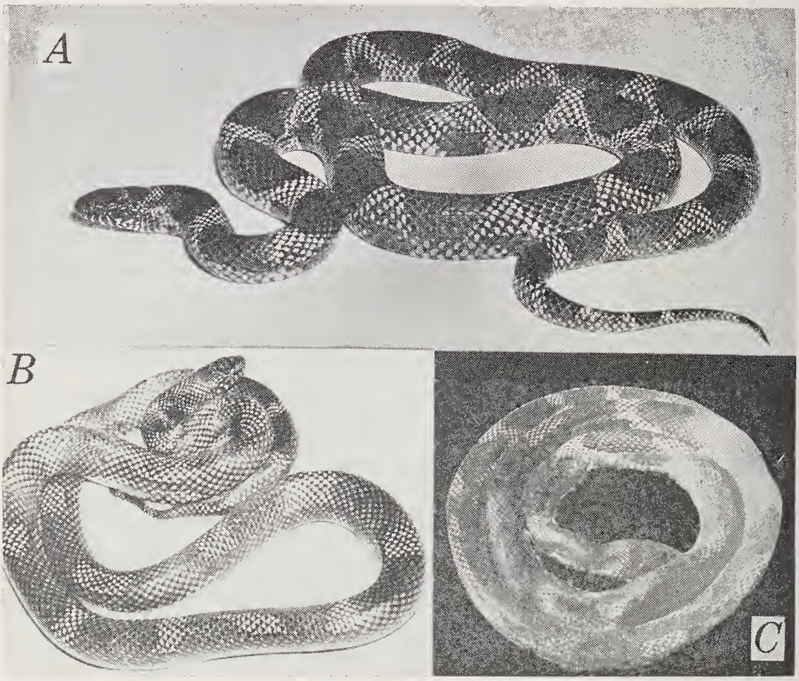


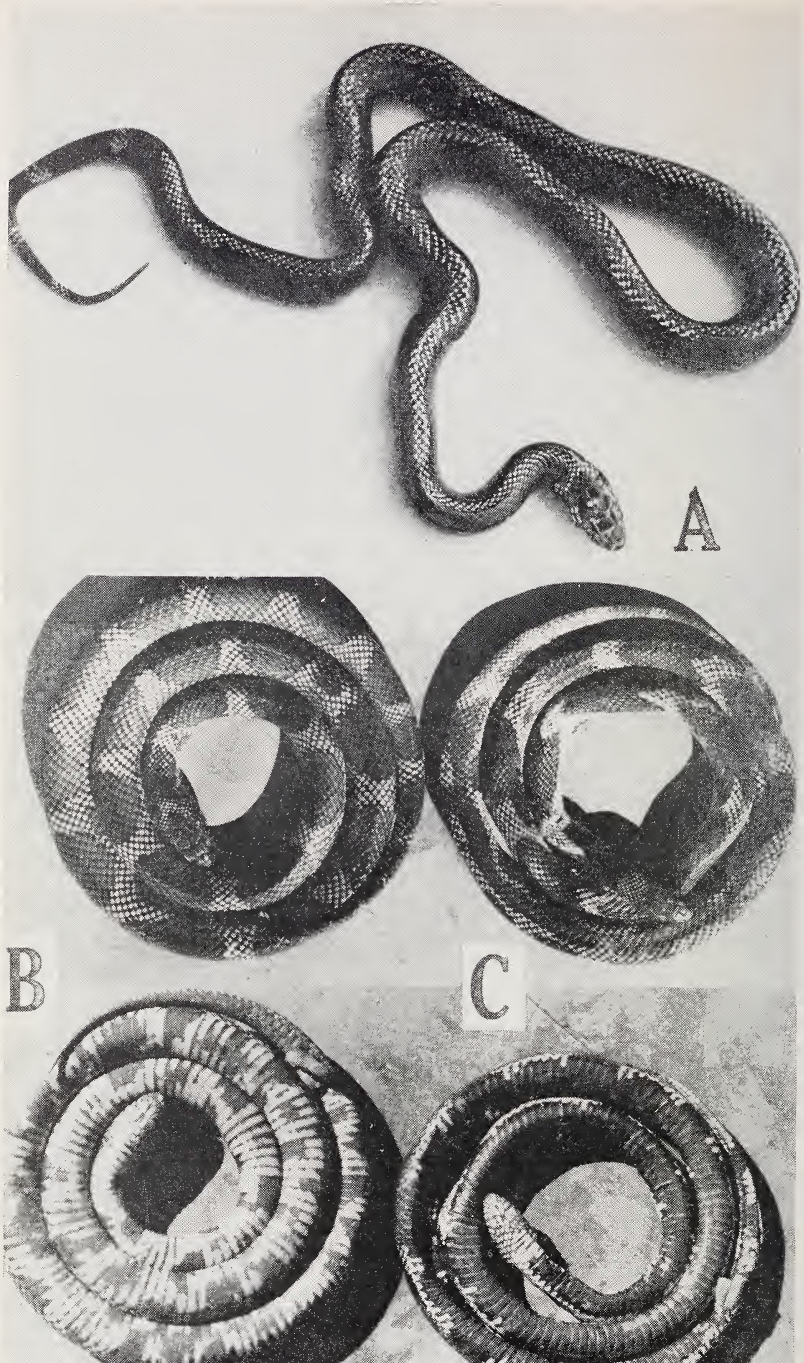
Fig. 1. Variation in *Lampropeltis getulus goini* from Gulf County, Florida. (A) Ringed pattern. (B) Light markings restricted to dorsum, suggesting a wide, broken vertebral stripe. (C) Mixed pattern of rings and stripes.

An extreme development of a lineate pattern is shown in WTN No. US-2558 from Cairo, Grady County, Georgia (Fig. 2, A). From the Cairo area I have seen about 20 kingsnakes, all more or less intermediate between *Lampropeltis g. getulus* and *L. g. goini*; and the present specimen may be considered as coming from an intergradient population. The markings include a posterior series of five saddles, one being on the body and four on the tail. Otherwise, in pattern this example closely resembles the striped phase of *L. g. californiae*. A yellow stripe, mostly about three scale rows wide, begins on the nape and extends posteriorly along the dorsal midline almost the full length of the body. As in many lineate *californiae,* the edge of the vertebral light stripe is not straight, but is laterally offset at several points. A lateral light stripe begins at the head and extends about a quarter of the length of the body; otherwise the sides are black, unmarked. In both *L. g. getulus* and *L. g. goini,* the venter is normally light-spotted, but in the present individual it is wholly black. In *californiae,* a wholly black venter is found only in the striped phase (Smith, 1943). The specimen is a female; and about 84 per cent of black-bellied *californiae* are female (Klauber, 1939). In *L. g. getulus* and *L. g. goini* there are usually some light markings on the underside of the tail; but in No. US-2558 the subcaudal region is completely black. In *californiae,* a black subcaudal region is always present in the lined, but never in the ringed, phase (Klauber, 1936; Smith, 1943).

Thus, No. US-2558, from the edge of the *Lampropeltis getulus goini* range, exhibits most of the peculiarities of the striped phase of *L. g. californiae;* while other *goini* and examples of *L. g. getulus,* as well as *L. g. sticticeps* if this latter prove valid, resemble the *californiae* intermediates which Klauber (1939) figured under the headings of "broken stripe" and "mixed ringed and striped." In *goini,* as in *californiae,* a dark, unspotted venter is found only in association with a strong tendency toward a lineate dorsal pattern (Fig. 2, B, C). Almost surely the same genic mechanism, at work in southern California, is also responsible for the occasional development of a wholly or partially lineate dorsal pattern, and a dark venter, among kingsnakes of the eastern United States.

The occurrence of a lineate pattern in both eastern and western subspecies of *Lampropeltis getulus* is not readily explained by a theory of interspecific hybridization in the past. Such a theory would imply that two distinct but closely related species of kingsnakes, one ringed and the other striped, once ranged sympatrically from the Atlantic to the Pacific; that the striped one in the range of *L. g.* "*boylii*" showed all the *boylii* characters except pattern, in the range of *L. g. goini* showed the *goini* characters except pattern, etc.; and that the striped one somehow blended into the ringed one everywhere, to a greater or lesser degree depending on locality.

Fig. 2. Variation in *Lampropeltis getulus goini.* (A) Almost full development of lineate pattern in WTN No. US-2558 from Cairo, Grady County, Georgia. (B) Dorsal pattern without lineate tendency, venter light-spotted in WTN No. US-2559 from Wewahitchka, Gulf County, Florida. (C) Dorsum with strong lineate tendency, venter predominantly dark in WTN No. US-2560 from Wewahitchka.


A
B
C

It is much more reasonable simply to postulate that a single widespread species, *L. getulus,* has the genetic potentiality of producing a lineate pattern along with the more common ringed one.

POLYCHROMATISM IN OTHER SNAKES

Time has shown that Klauber was correct in suggesting that *Masticophis flagellum frenatum* and *M. piceus* were but color phases; and this also proved to be the case with *Sonora miniata* and *S. semiannulata,* although *Phyllorhynchus browni* and *P. decurtatus* are still maintained as separate species. Smith (1952a) mentioned a possibility of dichromatism in the snake genus *Rhinocheilus.*

Smith (*idem*) also stated that there is an "unusual abundance in western United States, as compared with other parts of the continent, of dichromic snakes . . . " This statement has been widely accepted. However, to evaluate the contention one must first decide what constitutes ophidian dichromatism. Of course, dichromatism is but a simple form of polychromatism, which has been defined by geneticists, taxonomists, and students of several animal groups. But herpetologists, discussing pattern variants in American snakes, have usually ignored this body of literature. Hecht and Marien (1956), and J. M. Savage therein, are notable exceptions; they describe mimetic polychromatism in South American snakes of the genera *Oxyrhopus* and *Atractus.*

Riemer (1958) saw eight striped and five partially striped *Pituophis melanoleucus catenifer* from an area about 250 miles long, and concluded that there is a striped phase in this snake, comparable to the lineate phase of *Lampropeltis getulus californiae.* This conclusion is not challenged. But Riemer also set apart *P. m. catenifer* and *L. g. californiae* from all other snakes exhibiting the pattern alternatives, lineate vs. transverse, on the grounds that in all others the striped individuals occur "singly at unpredictable times and places." Should the existence of a dichromatic phase in *P. m. catenifer* have been ruled out if collections had chanced to yield, say, just three somewhat striped individuals, or just one? Should it have been ruled out if the actual specimens had come from an area three times as large, or ten times?

A partially or thoroughly lineate pattern has been reported as a rare to fairly common variant in many snakes that are usually blotched, ringed, or cross-banded. Examples include *Elaphe guttata emoryi, Lampropeltis c. calligaster, L. doliata gentilis, Sonora semiannulata isozona, Simophis rhinostoma, Agkistrodon c. contortrix, A. c. mokeson, Bothrops alternata, B. cotiara, B. jararaca, B. neuwiedii minasensis, B. n. pauloensis, Crotalus atrox, C. durissus terrificus, C. h. horridus, C. lepidus morulus, C. mitchelli stephensi, C. r. ruber, C. s. scutulatus, C. triseriatus aquilus, C. v. viridis, C. v. oreganus,* and *C. v. helleri,* as well as the hybrid combination *C. v. oreganus* X *C. s. scutulatus* (Amaral, 1932; Blanchard, *op. cit.;* Gehlbach, 1962; Gloyd, 1935, 1958; Klauber, 1956; Livezey, 1949; Stebbins, 1954).

To this list I can add *Elaphe g. guttata, E. obsoleta spiloides, Farancia a. abacura, Natrix e. erythrogaster, N. sipedon pleuralis, N. t. taxispilota* (Fig. 3), *Pituophis melanoleucus mugitus, Agkistrodon p. piscivorus, Crotalus horridus atricaudatus,* and *Lampropeltis d. doliata,* along with the previously mentioned eastern subspecies of *L. getulus.* The number of wholly or partially lineate examples known to me, from personal observation or from the literature, is one in *N. t. taxispilota,* three in *A. p. piscivorus,* 12 in *F. a. abacura,* 13 in *P. m. catenifer,* about 40 each in *P. m. mugitus* and *E. g. guttata,* etc.; but these figures are well-nigh meaningless for they do not necessarily give an idea of the frequency with which the lineate pattern occurs in nature. Most samples are small, and all are probably biased geographically. Even *L. g. goini,* with its relatively restricted range, is represented mostly by specimens from two small areas; and I have no idea what its pattern norm may be in, say, Wakulla County, Florida, whence Loftin (1962) reported a partially striped individual.

Of all snakes exhibiting a lined pattern as an alternative to a transversely marked one, only *L. g. californiae* has been sampled adequately. Klauber (1939) examined nearly 1,800 specimens from one county. Even this reptile has not been well studied in parts of its range. I believe the ratio of somewhat lined to normally blotched individuals actually is higher in *L. g. goini, E. g. guttata,* and *P. m. mugitus* than in *P. m. catenifer,* and that this ratio is exceedingly low in *N. t. taxispilota;* but other species probably fall between these extremes, and one cannot justify the selection of any point at which dichromatism begins. It is best to assume, in the absence of evidence to the contrary, that the above-listed cases, in which a snake exhibits a lineate pattern as an alternative to a more common transverse one, may all be comparable at least to a considerable degree.

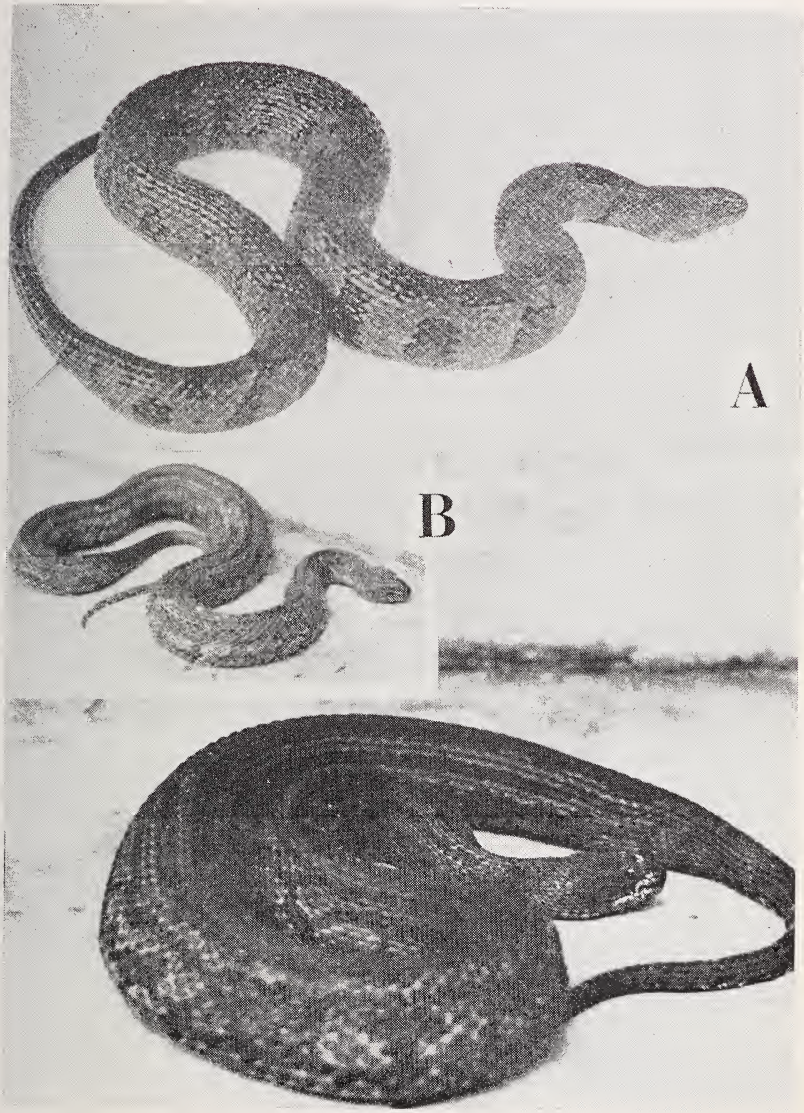


Fig. 3. Pattern phases of *Natrix t. taxispilota* from the Oklawaha River, Florida. (A) Common blotched phase. (B) Rare striped phase.

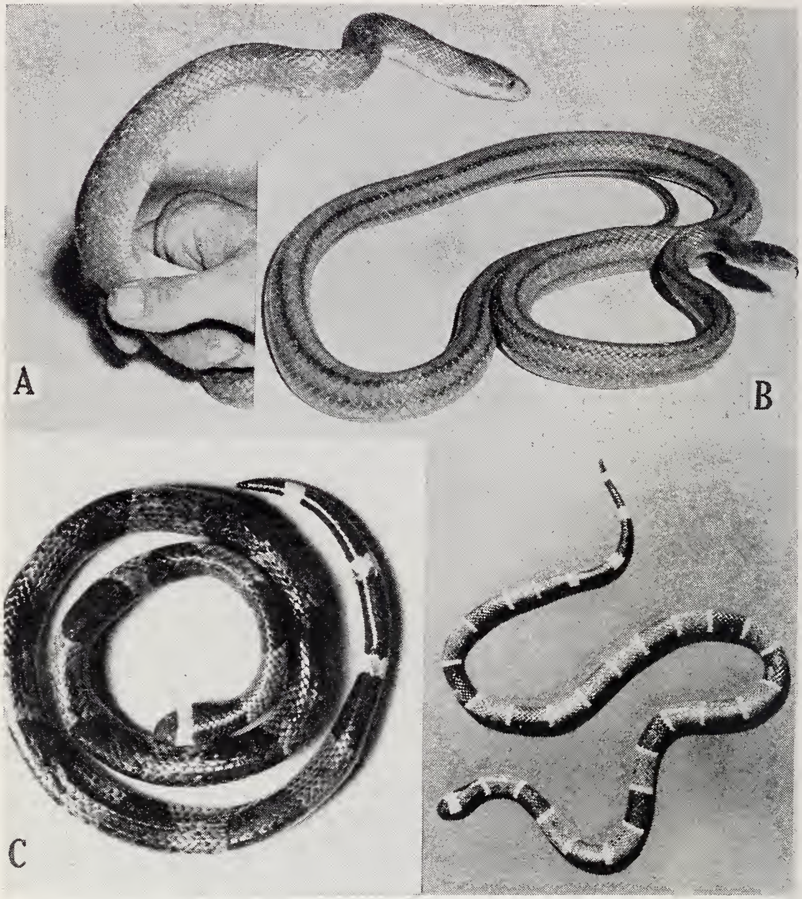


Fig. 4. Pattern dimorphism in snakes from peninsular Florida. (A) Uncommon unicolor phase and (B) common lined phase of *Elaphe obsoleta rossalleni.* (C) Uncommon saddled phase and (D) common ringed phase of *Micrurus f. fulvius.*

Some confirmation of this view may be provided by the tendency of the alternative lineate pattern to follow phylogenetic lines, as shown by the above list; and by the observation that a somewhat lineate pattern, rare in one species, may also occur rarely, or more commonly, or even as the norm, in a related species. Thus, lineate *Agkistrodon p. piscivorus* look much like the lineate *A. c. mokeson* and *A. c. contortrix* respectively figured by Gloyd (1958) and Livezey (*op. cit.*), there being an unmarked dorsum, a dark lateral band with a somewhat irregular upper edge, and the normal transverse markings on the neck, hinder body, and tail. The partially lineate pattern occurring occasionally in *Elaphe guttata emoryi* (Gloyd, 1935) and *E. obsoleta spiloides* is reminiscent of the normal condition in *E. g. rosacea,* some *E. o. lindheimeri,* and *E. o. williamsi* (Fig. 5); while in *E. o. quadrivittata* and *E. o. bairdi* the blotches are suppressed almost to the point of oblivion, leaving well-defined stripes. Several *Natrix* are normally striped, as are many species of closely allied genera. In hatchling *Farancia a. abacura* from peninsular Florida, the red ventral color extends up the sides to form rings, which may be complete but are usually somewhat interrupted dorsally. Occasionally, however, the red rings are reduced in regular fashion each to three dots, producing

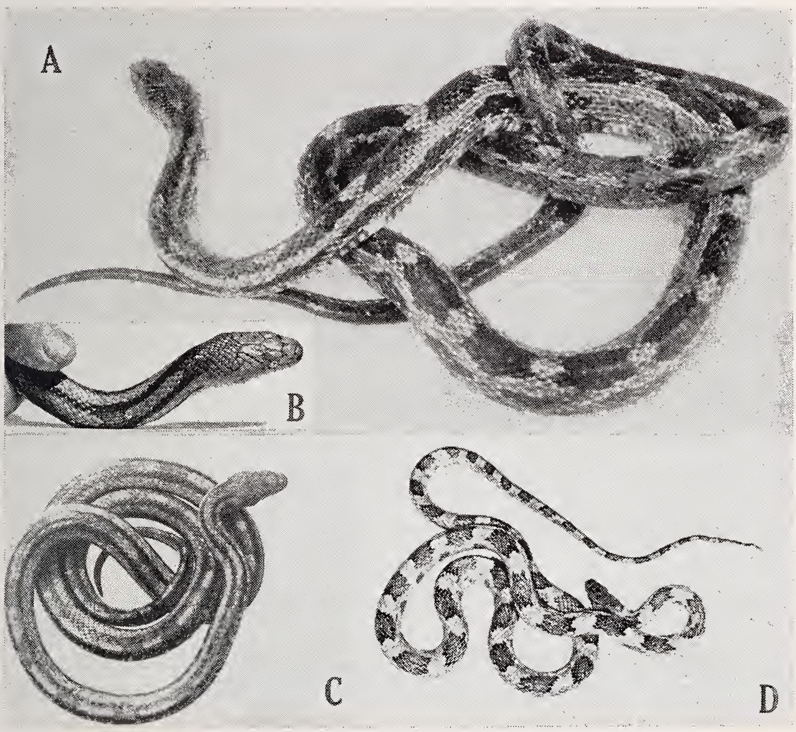


Fig. 5. Dichromatic alternatives in two related snakes. The common phase of *Elaphe obsoleta spiloides* is spotted (D). A specimen from Alabama exhibits an uncommon pattern of spots and lines (A). This latter pattern is the norm in *E. o. williamsi* from Levy County, Florida (B, C).

a dotted line down the back and one down each side of the reptile. In color and position these dotted lines are precisely like the complete stripes of *Abastor erythrogrammus*, a very closely related (actually congeneric) species.

Among the above-listed snakes, in which a lineate pattern exists as an alternative to a transversely marked one, there are seven that come from South America, and fifteen that inhabit eastern North America (excluding the subspecies of *Lampropeltis getulus*). This circumstance does not suggest any unusual concentration of dichromatic snakes in the southwestern United States. Furthermore, the discussion has so far been limited to the dichromatic alternatives, striped vs. transverse pattern; but other pattern alternatives are known. In his list of dichromatic snakes from the southwestern United States, Smith included the reptile now called *Masticophis flagellum piceus*, in which the alternatives are reddish vs. blackish. This red-black dichromatism is widespread among snakes. In species of eastern North America, it occurs throughout the wide range of *Storeria occipitomaculata;* and throughout the range of *Natrix sipedon compressicauda*, inhabiting south Florida coasts. It is found in *N. cyclopion floridana*, but only from a part of south Florida; in *Liodytes alleni* from scattered Florida localities; and in *Crotalus adamanteus*, but only from southwestern Georgia. In southern Mexico, *Stenorrhina freminvillei* has pinkish and grayish phases; in Central America, the reddish *Dryadophis sanguineus* is believed to be but an erythristic phase of *D. melanolomus alternatus*. I have not searched the literature for all reports of erythrism in usually blackish or grayish snakes, but cite Cooper (1948), Klauber (1956), Neill and Allen (1961), Stejneger (1907), and Wright and Wright (1957).

Sometimes there are more than two color phases. *Agkistrodon halys blomhoffi* is brown-banded at most localities on the main islands of Japan. A blackish phase is equally widespread but everywhere rare. A grayish phase is both rare and localized, being confined chiefly to Yamaguchi Prefecture on Honshu. A slate-colored phase occurs in Kagoshima Prefecture, Kyushu. A red phase is generally rare; but on Hachijojima, a small island south of Tokyo, it predominates. On this islet the black phase also occurs, but the common brown phase of the main islands is lacking. The distribution of all these variants has been worked out with considerable accuracy, because the Japanese popularly attribute a different medicinal value to the flesh of each phase, and afford legal protection to the especially prized gray one.

Ophidian pattern variations may be of many kinds. Limiting the discussion to species of the southeastern United States alone, one notes that *Urotheca flavilata* may be unicolor or weakly lined. *Natrix rigida* is occasionally melanistic (Etheridge, 1950). *Storeria occipitomaculata,* usually either blackish or reddish above, may occasionally be orange or yellow above; and the belly, usually red in both the reddish and the blackish phase, may occasionally be white, black, yellow, or parti-colored. *Thamnophis s. sirtalis,* generally provided with a lateral light stripe and a vertebral one, may at times lack either or both. In the Atlantic Coastal Plain population of *Lampropeltis g. getulus,* the ground color, usually brownish-black, may occasionally be yellowish, the yellow variant being at its most numerous in the region from Gainesville to Palatka, Florida; I have also seen one yellow individual of *L. g. goini,* and the discarded but probably valid subspecies *L. g. brooksi,* of southern Florida, is normally yellowish. *Elaphe obsoleta rossalleni,* usually marked with somewhat diffuse stripes, is sometimes unicolor (Fig. 4, A, B). *E. g. guttata,* usually marked with reddish and black, in many parts of Florida may completely lack the black. *Lampropeltis d. doliata* is generally marked with red, black, and yellow rings; but in parts of Florida the black rings may fuse longitudinally along the dorsal midline, and in other areas of the state all black markings may be absent. The lateral stripe in *Liodytes alleni* may be greenish, yellowish, orange, or lacking. *Pituophis melanoleucus mugitus,* strongly spotted as a norm, may also be a pale uniform tan, or a uniform medium brown, or weakly striped, or marked with weak stripes and strong spots, or so heavily suffused with black as to obscure any pattern; all these variants occur in peninsular Florida. In many areas the ground color of *Agkistrodon p. piscivorus* may be brown, olive, or black. *Crotalus h. horridus* is well known to have a yellowish and a blackish phase, with occasional intermediates. In *C. h. atricaudatus* the lateral ground color may be pinkish, gray, or yellow. In *Farancia a. abacura* the ventral ground color is normally red or pink; but a white-bellied variant has been reported at scattered localities from central Florida to North Carolina (Brimley, 1909; Hellman and Telford, 1956; Wright and Bishop, 1915). *Opheodrys aestivus* has both a yellow-bellied and a green-bellied variant in Florida and Georgia; a white-bellied variant is also known. *Crotalus adamanteus,* usually with a pattern of dorsal diamonds, is occasionally marked with narrow transverse bands, somewhat as in *C. tigris;* and I have seen one grayish, patternless individual precisely like the aberrant *C. atrox* figured by Gloyd (1958). *Micrurus f. fulvius* has a black-saddled, rather than black-ringed, phase (Fig. 4, C, D) in Florida (Meachem and Myers, 1961). *Natrix sipedon fasciata, N. s. pictiventris,* and *Heterodon platyrhinos* are described in the literature simply as "very variable," but at any given locality most specimens can be sorted into about four or five categories; some of the variation is discontinuous, *i.e.,* polychromatic. Wright and Wright *(op. cit.)* have described many pattern variants of North American snakes.

Recent investigation of snakes from southern Mexico and northern Central America suggests frequent occurrence of polychromatism in that region. Reference has already been made to the reddish vs. grayish dichromatism in both *Dryadophis melanolomus* and *Stenorrhina freminvillei;* the latter also seems to have lined and unlined phases. *Loxocemus bicolor* is dichromatic as regards ventral coloration, while *Conophis lineatus* has lined and unlined phases (Neill and Allen, *op. cit.*). To this list may probably be added *Ficimia ramirezi,* known from but a single specimen, collected in the range of *F. publia* and differing therefrom only in that the dorsal blotches are reduced in size; several other snakes are known to produce a variant with much reduced dorsal blotches. *Ninia s. sebae* has one phase with a nearly immaculate red dorsum, and another with transverse red, black, and yellow bands the full length of the body. Both phases, and intermediates, are common in British Honduras. The British Honduras coral snake, *Micrurus affinis,* a close relative of the Floridian *M. fulvius,* like the latter occasionally displays black saddles instead of rings; the saddled form in British Honduras was once given taxonomic recognition but does not seem to predominate anywhere.

I have made no extensive search of the literature relating to polychromatism in Old World snakes, but call attention to Leeson's (1950) illustration of pattern phases in the African colubrid *Psammophis sibilans,* and his remarks on the existence of three equally common color phases (green, blue, and gray) of *P. elegans;* Mao's (1962) account of lineate and brown-banded examples of the Asiatic elapid *Bungarus multicinctus,* usually cross-banded with black on a whitish ground; Gans's (1959) analysis of nine color phases among the two species of the African colubrid genus *Dasypeltis;* Mertens's (1955) portrayal of pattern phases in the African viperid *Bitis caudalis;* Bogert's (1940) discussion of a red phase of the usually grayish African elapid *Naja nigricollis,* and Loveridge's (1929) observation that this snake may also be "black, brown, khaki, olive, [or] bluish-gray, with or without markings;" Minton's (1962) figures showing several patterns of the Asiatic colubrid *Spalerosophis arenarius;* and Taylor and Weyer's (1958) notes on two phases of the African boid *Calabaria reinhardti.* Polychromatism appears to be widespread among snakes, from both geographic and phylogenetic standpoints.

DISCUSSION

It should be clear from the foregoing account that among snakes, a polychromatic variant may be very rare, fairly common, or very common in collections; as common in nature as its alternative, somewhat less common, or much rarer; widely distributed, somewhat restricted, or highly localized. This is not to contend, however, that every pattern variation in snakes should be ascribed to polychromatism.

Some variations are continuous, gradational; while by definition polychromatic variants must be discontinuous.

Some variations may also be purely phenotypic, although pattern peculiarities in snakes have rarely been linked with any environmental factor. Elsewhere I have pointed out that species of amphibians and reptiles, characteristic of inland situations, sometimes take up residence in salt-water habitats, such as strand, mangrove swamp, or salt marsh, and the individuals of these salt-water populations are apt to show color peculiarities resulting from an increase in melanin pigments (Neill, 1958). Although it is not certain that this effect is wholly environmental, I believe it to be. Simmons and Stine (1961) raised a brood of three eggs from the North American colubrid *Carphophis a. amoenus.* All the eggs became desiccated; and two of the young, upon hatching, were of normal coloration (brown above and pink below) but exhibited ankylosis of the spine at the points where the embryo was flexed within the shell. The third young was not ankylotic but was thoroughly xanthic, yellowish above and cream below. Simmons and Stine thought the xanthism was probably not the result of egg dehydration; but further investigation is needed.

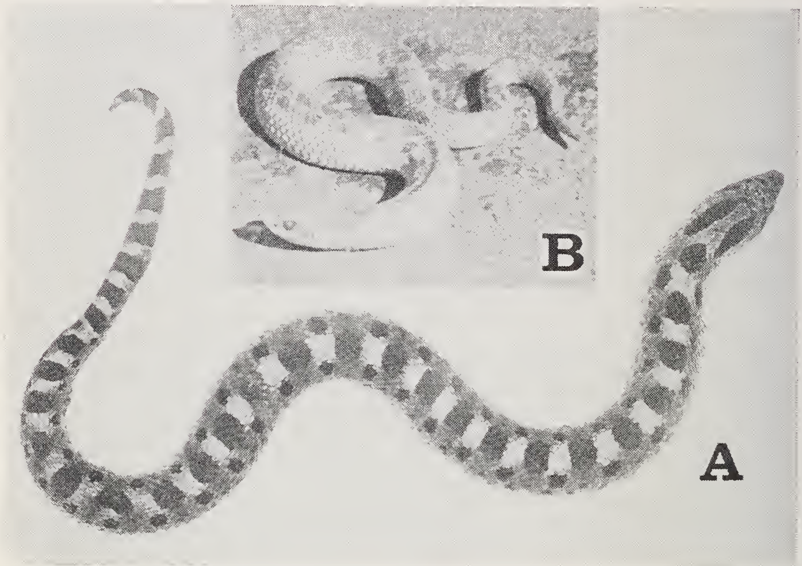


Fig. 6. A selectively disadvantageous pattern variant in *Heterodon simus* from central Florida. The normal pattern (A) is camouflaging, perhaps mimetic (of the venomous *Sistrurus miliarius barbouri*), and is produced by melanin deposits which probably facilitate thermal flux and screen against components of solar radiation. The leucistic pattern (B) is less effective in all these regards.

Some variations, discontinuous and of genetic origin, are so extreme as to jeopardize the existence of the variant individual, and render improbable the persistence of the variation (Fig. 6). The most familiar example of an extreme, selectively disadvantageous variation is albinism. It has been reported in 25 species of snakes from North America alone (Hensley, 1959), but none of these has produced an albinistic population in nature. Nevertheless, such populations are readily bred in captivity; and a wild population of albinistic *Elaphe climacophora* has developed at Iwakuni, Japan, partly in consequence of ecological isolation, but mainly as a result of artificial selection by local residents who regard white snakes as sacred (Choate, 1963). Thus even an extreme variation, normally disadvantageous, under exceptional circumstances could be the start of a polychromatic phase. As a general rule, however, the rarer of two pattern phases in one species is apt to be the usual pattern in some other species. Such characters as white venter, vertebral light stripe, unicolor dorsum, blackish suffusion, dorsal saddles, etc., each occurs in some one species only as a variant, but each also occurs as a norm in many other species.

Grotesque, often asymmetric patterns, as in a *Farancia* figured by Etheridge (*op. cit.*), or a vitiliginous *Crotalus* shown by Gloyd (1958), must be highly disadvantageous, to judge from their rarity. Extremely aberrant patterns are found much more often among juvenile snakes than among adults, as Blanchard (*op. cit.*) long ago found to be the case in the kingsnake genus *Lampropeltis*. E. R. Dunn (1942) and later authors have shown that among snakes generally, there is apt to be selection against even some slight variations of pattern and scalation; and it may be that certain seemingly minor variations are accompanied by disadvantageous peculiarities of behavior or physiology. In several neonatal snakes some obvious anatomical abnormality has been found to accompany a highly aberrant pattern (Fig. 7).

Although little is known of ophidian genetics, many cases of polychromatism, in animals other than snakes, are quite reminiscent of the situation in these reptiles; and it seems probable that but a single biological phenomenon is involved. For example, in the mouse, the genetics of which has been intensively studied, certain color variations are known to be associated with selectively disadvantageous conditions, such as peculiarities of gait, anemia or other blood disorders, ankylosis of the caudal vertebrae, microphthalmia, and abnormalities of the reproductive system.

The "burnsi" (unspotted dorsum) dominant mutant of the usually spotted frog *Rana p. pipiens* is mostly localized in a small area; the phases are inherited in mendelian fashion although with modifiers that sometimes limit the expression of the unspotted pattern (Moore, 1942; Volpe, 1960). Similarly, the striped phase of *Lampropeltis getulus californiae* is mostly localized in a small area; the striped and ringed phases are believed to be inherited in mendelian fashion but with modifiers that sometimes limit the expression of the lineate pattern (L. C. Dunn, *op cit.*). The "kandiyohi" (mottled dorsum) dominant mutant is localized in *R. p. pipiens,* is of rare and scattered occurrence in some other *Rana,* but is the norm in *R. areolata* (Anderson and Volpe, 1958; Moore, 1943, Volpe, 1955); just as the saddled (as opposed to ringed) pattern is rare and scattered in *Micrurus fulvius,* is localized in a British Honduras population of the closely related *M. affinis,* and is the norm in another relative, *M. bernadi.*

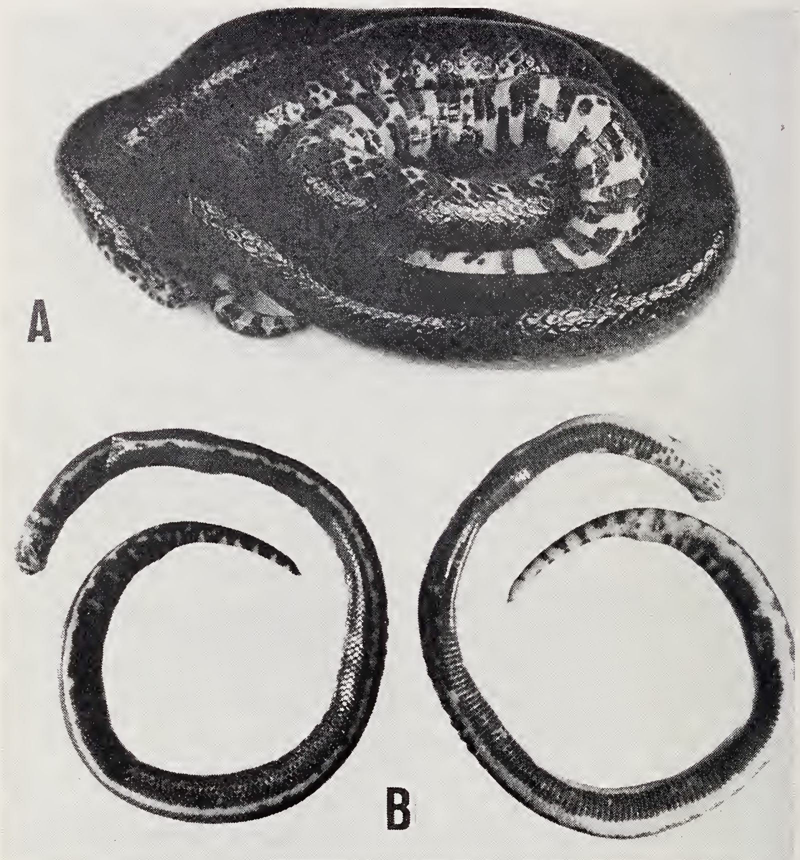


Fig. 7. An extreme pattern variant associated with an anatomical abnormality in *Farancia a. abacura* from central Florida. The normally patterned individual (A) is black except for red ventral areas which extend onto the sides. In an aberrant hatchling (B), there is a vertebral red stripe with notched edges, a light nuchal collar, narrow light bars on the hind part of the body, and a mid-ventral black stripe with light borders. The spectacle of each eye is enlarged and bulging.

The dichromatism, reddish vs. blackish, occurs not only in snakes but in such diverse groups as primates, felines, rodents, hawks, owls, lizards, toads, salamanders, and beetles.

A certain polymorphic butterfly mimics a distasteful species, but only in one pattern phase, the numerical ratio of this phase being highest in areas where the model occurs (Carpenter, 1920). In another butterfly, two polymorphic variants each mimic a different model (Ford, 1940).

Roughly comparable is the situation in *Ninia s. sebae,* a harmless snake which closely resembles the venomous *Micrurus affinis.* The mimic, at least in British Honduras where I have studied it, almost always exhibits transverse dorsal markings of red, yellow, and black in areas where the model is so marked; but where the model exhibits a reduction of its black and yellow rings to dorsal saddles, the ringed phase of *Ninia* is rare, most specimens exhibiting a reduction of the black and yellow equaling or exceeding that of the *Micrurus.* Goldschmidt (1945) speaks of the important relationship between mimicry and polychromatism.

Of course, this is not to say that snakes will yield no new information about polychromatism. These reptiles may exhibit peculiarities not often found in other animals. Thus, little is known of the forces regulating the numerical ratio of one polymorphic alternative to another. Ford (*op. cit.*) believed that polymorphic alternatives would very rarely be of equal selective value; but Mayr (1942) held that in many animals, alternative patterns are likely to be selectively neutral. Snakes should provide excellent material for an analysis of selective forces operative upon polychromatic pattern phases. For example, a striped pattern is found as a normal condition mainly in snakes that are (1) slender and very active; (2) dwellers in open places, or grassy ones; (3) arboreal among vines, twigs, and small branches; (4) primarily aquatic; or, rarely, (5) primarily subterranean; while a transverse pattern characterizes sluggish to moderately active snakes, of moderate to heavy build and living a primarily terrestrial existence in wooded areas. The eastern subspecies of *Lampropeltis getulus* belong in the latter category, and in these kingsnakes one would expect natural selection to militate against a fully lineate pattern. I am not familiar with *L. g. californiae* in the field; but Klauber (1939) found that, in this subspecies, the percentage of lined individuals was higher in captive-hatched broods than in nature, and that the lined phase was to some degree excluded from certain habitats where the ringed phase flourished. Both these findings imply that the lineate pattern is selected against in parts of California. The genetics and natural history of the kingsnake are so poorly known that one could not suggest why the striped phase has not vanished completely; fortunately, Fisher (1930) has provided a theoretical explanation for the persistence of a disadvantageous polymorphic variant.

The emphasis in herpetological literature (*e.g.*, Smith, 1952a) upon hybridization, or at least upon a recombination of former isolates with drift-induced differences, as a theoretical explanation of polychromatism in snakes, apparently stems from difficulty in understanding how a mutant color pattern, not especially advantageous selectively, could spread other than in isolation. That such spread is possible without isolation has been shown by Fisher (*op. cit.*); Kojima and Kelleher (1962) provide a more recent analysis of the topic. Of course, this is not to rule out entirely the isolation-drift-recombination sequence as a theoretical explanation for some pattern variation in snakes; but it does not seem often to have been invoked by students of polymorphism in general.

SUMMARY

A kingsnake, *Lampropeltis getulus californiae,* in southern California may be either ringed or striped, both phases sometimes occurring in a single brood. The situation is generally conceded to be one of dichromatism in a single species, but has also been ascribed to hybridization of two distinct species differing only in pattern. Dichromatism has been reported in several other snake species of the southwestern United States, and it has been contended that something in the past environment of that region has been egregiously conducive to the development of dichromatism in these reptiles.

However, it is pointed out that dichromatism is but the simplest form of polychromatism, a geographically widespread phenomenon among snakes and among many other organisms. The condition in *Lampropeltis getulus* finds many parallels, and the western United States harbors no unusually high percentage of polychromatic snakes.

Neither the distribution nor the relative abundance of a pattern variant will *per se* rule out its consideration as an example of polychromatism. Pattern variants in snakes are to be considered polychromatic unless they are of a continuous, gradational nature, or are of environmental origin. Even an extreme variation, such as

albinism, has at least the potentiality of initiating a polychromatic phase, although this is likely to take place only under exceptional circumstances.

Geneticists, taxonomists, and students of animal groups other than snakes, have often investigated polymorphism (of which polychromatism is a common form). These workers have provided a framework of fact and theory into which it is often possible to fit some of the facts regarding pattern variants in snakes. Of course these reptiles may also provide new information about polymorphism, and especially about the forces that determine the numerical ratio of polychromatic alternatives in nature.

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122 Homecrest Road, New Port Richey, Florida.